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Luminance contrast has little influence on the spread of object-based attention

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ABSTRACT

We direct our attention to those visual stimuli that are relevant to our behavioral goals. Some of the visual stimuli that surround us are represented more strongly, because they have a higher luminance contrast. However, selective attention also boosts the representation of visual stimuli. It is not yet well understood how attention and contrast interact. Some previous theories proposed that attentional effects are strongest at low contrast, others that they are strongest at high contrast and yet others that the effects of selective attention are largely independent of contrast. In the present study, we investigated the interaction between selective attention and luminance contrast with a contour-grouping task that provides a sensitive measure of the spread of object-based attention, with delays of several hundreds of milliseconds. We find that the spread of object-based attention is largely independent of contrast, and that subjects experience little difficulty in grouping low-contrast contour elements in the presence of other contour elements with a much higher contrast. The results imply that object-based attention and contrast have largely independent effects on visual processing.

1. Introduction

Our visual system initially decomposes the visual image that falls on our retinas into many image fragments. The receptive fields in the retina and in the pathways that propagate the information to the visual cortex are small and each neuron therefore represents only a small piece of the visual world. This fragmentation is preserved at the first few stages of cortical information processing. Neurons in early areas of the visual cortex have small receptive fields and represent one or only a few visual features, such as the orientation, color or motion of the image element in their receptive fields. However, we do not perceive such a fragmented image. The visual objects of our perceptual world are spatially extended and composed of many features. There are apparently powerful perceptual organization processes at work for the grouping of image elements into object representations, and for the segregation of these features from those that belong to other objects and the background.

Higher visual areas contribute to perceptual grouping because neurons in these areas have large receptive fields and are tuned to more complex feature constellations. Some neurons in the inferotemporal cortex, for example, code the shape of a face and their activity implicitly groups face-features, like eye, nose and mouth into a whole (Tsao, 2006; Freiwald, Tsao, & Livingstone, 2009). The grouping of complex feature constellations by dedicated neurons has been called 'base-grouping' (reviewed by Roelfsema, 2006; Roelfsema & Houtkamp, 2011). Base-grouping can occur in parallel across the visual scene and is fast because it relies on the rapid phase of feedforward processing from lower to higher visual areas that occurs immediately after the presentation of a visual image (Hung et al., 2005; Thorpe, Fize, & Marlot, 1996). At a psychological level of description, base-grouping is therefore thought to correspond to 'pre-attentive vision', i.e. the set of visual processes that can occur without attention (Neisser, 1967; Roelfsema, 2006). However, there are limitations to base-grouping. Base-grouping can presumably only work for familiar objects, not for novel feature constellations for which there are no dedicated neurons in higher visual areas. If the object is unfamiliar, an additional 'incremental-grouping' process has to be invoked, which labels all to-be-grouped image elements with object-based attention. This labeling process can group new feature constellations by labeling the individual features represented in lower visual areas, but this additional flexibility comes at the cost of longer processing times (Roelfsema, 2006; Roelfsema, Tolboom, & Khayat, 2007; Roelfsema & Houtkamp, 2011).

One task that has been used to study incremental grouping is the curve tracing task illustrated in Fig. 1A. Suppose that you

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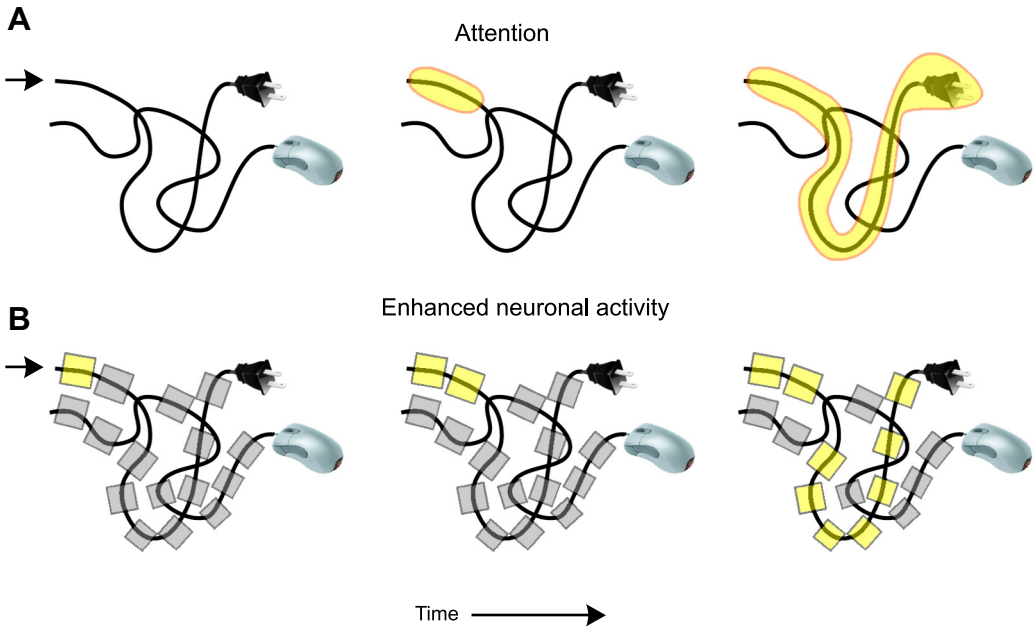

Fig. 1. Incremental grouping of contour elements in the curve-tracing task. (A) Contour grouping task. In order to group the contour elements that are part of one of the cables, object-based attention (yellow) spreads over one of the curves until the entire object is labeled with attention and the plug can be identified. (B) Neurons in the visual cortex increase their response if their receptive fields (rectangles) fall on the relevant curve and they spread the enhanced neuronal activity along this curve.

would like to know if the upper cable is connected to the plug or to the computer mouse. This is a perceptual grouping task, which is solved once you know which contour elements belong to one of the cables. Moreover, it is likely that you have not seen curves with this particular shape before and, accordingly, there may be no neurons in higher visual areas that code these shapes. Yet, observers do not experience problems with this task.

Previous studies showed that object-based attention gradually spreads along the relevant curve until it is entirely labeled with attention (Houtkamp, Spekreijse, & Roelfsema, 2003; Scholte, Spekreijse, & Roelfsema, 2001). Thus, object-based attention acts to group all contour elements of one of the cables into a coherent representation. The time-consuming nature of incremental grouping is reflected by the pattern of reaction times in the curve-tracing task. The reaction time increases approximately linearly with the length of the curve for which elements have to be grouped, with processing delays that can increase up to several hundreds of milliseconds (Crundall, Cole, & Underwood, 2008; Jolicoeur & Ingleton, 1991; Jolicoeur, Ullman, & Mackay, 1986, 1991; McCormick & Jolicoeur, 1992; Pringle & Egeth, 1988; Roelfsema, Scholte, & Spekreijse, 1999).

A neuronal correlate of the spread of object-based attention can be measured in low-level areas of the visual cortex of monkeys (Roelfsema, 2006; Roelfsema, Lamme, & Spekreijse, 2004). Attended image elements evoke stronger neuronal responses than non-attended image elements in visual cortex (reviewed by Desimone & Duncan, 1995; Reynolds & Chelazzi, 2004) and during curve-tracing an attentional response enhancement gradually propagates along the representation of the relevant curve in the visual cortex until it is entirely labeled with enhanced neuronal activity (Fig. 1B), an effect that can also be measured in the EEG of human observers (Lefebvre et al., 2011; Lefebvre, Jolicoeur, & Dell'Acqua, 2010). The selectivity of this labeling process is thought to rely on the architecture of corticocortical connections. Nearby neurons in the visual cortex are likely to be linked by horizontal connections if they code contour elements that are in each other's good continuation (Bosking et al., 1997; Schmidt et al., 1997), and these connections may therefore cause the selective spread of object-based attention. Indeed, when attention is directed to a contour element, the enhanced response spreads from this element to adjacent image elements that are related by good continuation or by other Gestalt grouping cues (Wannig, Stanisor, & Roelfsema, 2011). Theories of curve-tracing therefore that neurons in the visual cortex receive the enhanced response from neurons with receptive fields at an earlier position on the curve to then propagate it onwards, to neurons with receptive fields farther along the curve (Fig. 1B) (Jolicoeur, Ullman, & Mackay, 1991; Sha'ashua & Ullman, 1988; Grossberg & Raizada, 2000; Roelfsema, 2006). In curve-tracing, this propagation has to be gradual because only nearby contour elements are in each others' good continuation, whereas contour elements of the same curve which are farther apart can be in any arbitrary configuration. The enhanced response therefore has to propagate gradually, across all the intermediate contour elements before it can reach the end of the curve. Previous studies demonstrated that the signals for object-based attention in early visual areas are strong and reliable. Only a few cells in the primary visual cortex suffice to distinguish between image elements that are attended and those are not on a single trial (Poort & Roelfsema, 2009). The participation of neurons in early visual cortex with their high spatial resolution (small receptive fields) in curve tracing is thought to be beneficial if the relevant curve runs close to other curves.

However, attention is not the only factor that influences neuronal activity in early visual cortex. Changes in the contrast of a stimulus have an even more pronounced effect on activity in early visual cortex than shifts of visual attention. If curve-tracing depends on the propagation of enhanced neuronal activity in visual cortex, it might be dominated by high contrast stimuli. Is it more difficult to trace a low contrast curve in the presence of high contrast curves (Fig. 2A)? If not, is it possible that the neuronal codes for attention and contrast differ in low-level areas? One difference between the neuronal codes for contrast and attention is that virtually all visual cortical cells increase their response for stimuli with a higher contrast but that not all cells are modulated by attention. There is a set of non-modulated cells (N-cells) that are uninfluenced by attention. The presence of these N-cells has a number of advantages. First, they could provide

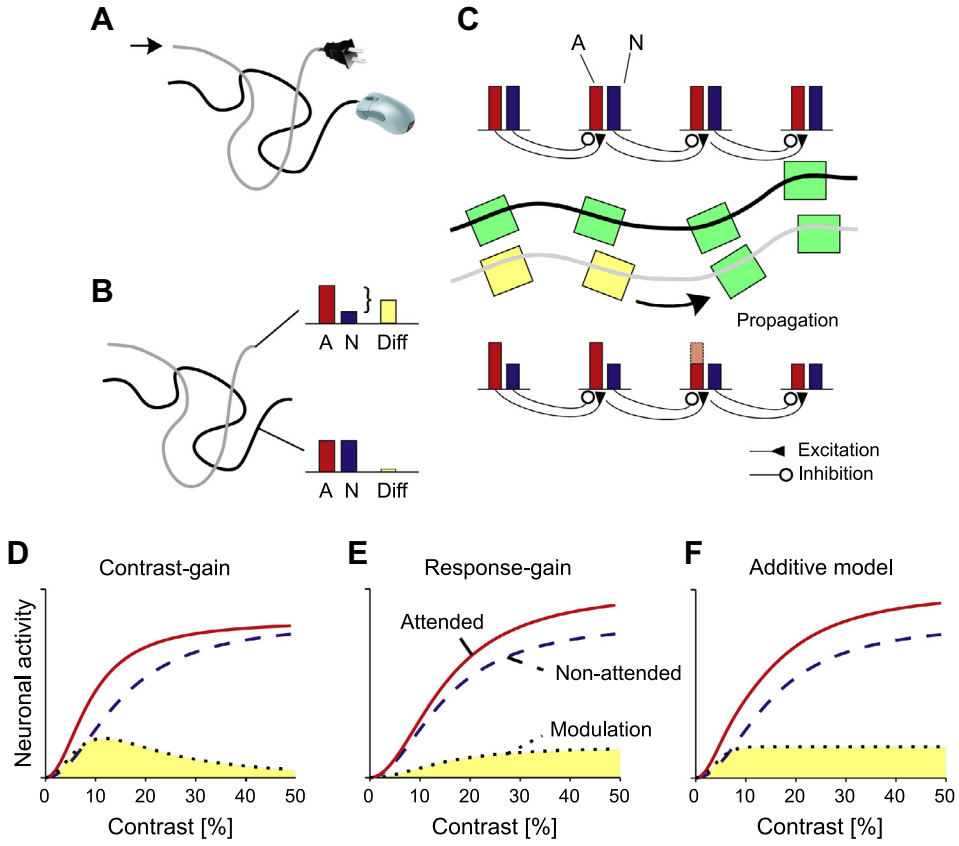

Fig. 2. Influence of contrast variation on contour-grouping. (A) It is possible to trace a curve that is of relatively low contrast in the presence of another curve with higher contrast. (B) The activity of N-cells (blue) in the visual cortex only depends on contrast, whereas the activity of A-cells depends on contrast and also on attention. A previous model proposed that the difference between A- and N-cell activities could index attentional selection irrespective of the contrast of the curves. In the example, the low contrast curve is attended so that the A-cells have a higher activity than the N-cells. (C) It is possible to propagate a difference in the level of activity of A and N-cells along the curve (yellow receptive fields). In the example connection scheme, A-cells excite other A-cells that respond to contour elements farther along the curve, whereas N-cells have an inhibitory effect on adjacent A neurons. Note that excitation and inhibition is balanced for A-cells that respond to the upper curve. (D–F) Three models describing the conjoined effect of contrast and attention on neuronal activity in the visual cortex. (D) Contrast gain model. Attention shifts the contrast response function to the left (red curve). Note that effect of attention on neuronal responses (yellow area) is most pronounced at low contrasts. (E) Response-gain model. Attention scales the contrast response function and has strongest effects at higher contrasts. (F) Additive model. Attention adds activity to the neuronal response in a manner that is relatively independent of contrast.

a veridical representation of stimulus contrast, irrespective of attention shifts. Second, N-cells permit the representation of the locus of attention in early visual areas in spite of variations in stimulus contrast, because the activity of A-cells that are modulated by attention can be compared to the activity of N-cells. For an attended stimulus, the activity of A-cells is always stronger than the activity of N-cells, irrespective of luminance contrast (Fig. 2B). A recent study demonstrated that the population of V1 neurons indeed represent the contrast of a stimulus as well as the locus of attention, in accordance with a coding scheme with N- and A-cells (Pooresmaeili et al., 2010). Roelfsema and Houtkamp (2011) suggested that it is the difference in activity between A-cells and N-cells that propagates along the target curve (Fig. 2C). The propagation of enhanced A-cell activity could rely on a connection scheme where A-cells excite neighboring A-cells though horizontal connections whereas N-cells inhibit neighboring A-cells. Unattended contour elements evoke similar activity of A- and N-cells and neurons coding adjacent image elements therefore receive balanced excitation and inhibition. However, A-cells are more active than N-cells for the attended contour elements, and this enhanced activity could therefore propagate to A-neurons coding contour elements farther along the curve.

Even if the difference in activity of N- and A-cells determines the propagation of object-based attention, there may still be a residual influence of contrast on the efficiency of curve-tracing, because the magnitude of the attentional signal could depend on the contrast of the stimulus. According to the so-called "contrast-gain" model (Fig. 2D), attention increases the activity evoked by a visual stimulus by increasing its apparent contrast (Martınez-Trujillo & Treue, 2002; Reynolds, Pasternak, & Desimone, 2000; Treue, 2004). Attention would shift the contrast response function to the left. According to this model, attention strongly influences the representation of stimuli of intermediate contrast but has a weaker effect at high contrasts, where the contrast–response function has saturated. However, other studies showed that shifts in the contrast-response function do not describe the effects of attention on the activity of all cells in visual cortex. Williford and Maunsell (2006) demonstrated that attention and contrast interact in a multiplicative manner for a substantial fraction of the neurons. In these cells attention scales the entire contrast response function by a factor (Fig. 2E). In such a "response-gain" model, attention has strongest effect on neuronal firing rates (and thus on the difference in activity of A- and N-cells) at the higher contrasts.

A third model for the interaction between attention and contrast is an additive model. fMRI studies have demonstrated that the effects of attention and contrast are approximately additive once the stimulus has sufficient contrast to be perceived (Buracas & Boynton, 2007; Pestilli et al., 2011) (Fig. 2F). These results are supported by a neurophysiological study that compared the three models of Fig. 2D–F in primary visual cortex. This study revealed that the "additive model" was best able to account for the effect

of attention on neuronal firing rates (Thiele et al., 2009). Although the results of these previous studies seem to diverge, a recent model showed that some of the discrepancies can be resolved by considering differences in the size of stimuli relative to the window of attention (Boynton, 2009; Herrmann et al., 2010; Reynolds & Heeger, 2009).

The present study investigated how contrast variations influence the efficiency of contour grouping. The strong increase in reaction time with the length of a traced curve implies that the curve-tracing task provides a sensitive measure of the efficiency of object-based attention shifts. The aim of this study was to examine whether behavioral measures (the speed at which participants can trace curves) would support the hypothesis that there are separable neuronal codes for object-based attention and contrast. If these codes are indeed separable, the absolute contrast level should not matter for the efficiency of contour grouping. However, if they are not, it should be difficult, if not impossible, to trace a low contrast curve in the presence of a high contrast distracter curve (as would be required in Fig. 2A) leading to slower tracing speeds and many errors. Our second aim was to measure how the speed of contour-grouping depends on contrast, because it may distinguish between the different models of the interaction between attention and contrast. Assuming that curve tracing indeed depends on a propagation of enhanced activity along the curve (as proposed by Roelfsema & Houtkamp, 2011), this process should be most efficient when the difference between the activity of A and N-cells is large. The alternate models make different predictions about how contrast will affect the speed of curve tracing. For the contrast-gain model, tracing would be expected to be most efficient for curves with an intermediate contrast and least efficient at high contrasts where attention has only a small influence on the neuronal response (yellow area in Fig. 2D). The response-gain model, predicts the opposite outcome, because the attentional effect is stronger for higher contrasts and tracing should therefore be most efficient for high contrast curves (Fig. 2E). Finally, the additive model predicts that the efficiency of the attentional contour-grouping process should not depend strongly on contrast, at least as long as the contrast is high enough to make the curves visible (Fig. 2F).

2. Experiment 1: The effect of luminance contrast on the speed of contour grouping

To investigate the influence of luminance contrast on the speed of contour grouping we used a variant of the curve-tracing task that has been introduced by Jolicoeur et al. (1986, 1991). The influence of contrast on tracing speed was investigated in one experiment of McCormick and Jolicoeur (1992), who presented two curves at the same or at different contrasts. They observed that tracing speed did not depend strongly on contrast if both curves had the same contrast but that the task was solved very efficiently if the two curves differed in contrast. However, the values of the contrasts were not documented in that study and only two contrasts and two curves were used. Experiment 1 aimed to extend these findings with more levels of contrast. Participants saw two curved lines, one of which (the target curve) was connected to the fixation point (Fig. 3C). We used three values of contrast for the two curves and we presented a colored marker on each curve, one red and one green. Participants had to report the color of the marker on the target curve.

2.1. Methods

2.1.1. Participants

Ten participants were recruited (8 females, average age: 22.2 years). All had normal or corrected vision and had not participated in curve tracing tasks before. Ethical approval was obtained through the Ethics Committee at the University of Amsterdam. We obtained informed consent in writing from the subjects before the experiment started.

2.1.2. Stimuli and apparatus

The experiment was programmed with EventIDE stimulus presentation software on a PC. Participants were seated comfortably at a distance of 50 cm from a 50 cm Dell Trinitron monitor in a dimly lighted room with their head on a forehead/chin rest. The monitor had a frame rate of 100 Hz and a display size of 1024×768 pixels with stimuli extending up to 10 visual degrees from the central fixation point. Responses were registered using buttons on a gamepad.

The stimuli consisted of two curves (4 pixels thick) one of which was connected to a fixation cross (target curve). The curves were presented on a dark-gray background with a luminance of 18 cd/m^2. On every trial we presented a red marker on one of the curves and a green marker on the other, at corresponding positions on the two curves (t1 and d1, t2 and d2, or t3 and d3 in Fig. 3A). We varied the distance between the fixation point and the markers as measured along the path of the curve (t1, t2 and t3). The length of the path along the curve from the fixation point to t1 was 9.3°, there was 14.5° between t1 and t2 and 16.2° between t2 and t3. These three positions were all equidistant from the fixation point, on the circumference of an invisible circle with radius of 13.8° (Fig. 3A). Markers were 1.5° in diameter. In order to ensure that participants did not become familiar with the stimuli and thus could predict the location of the target marker without tracing, the stimuli were rotated around the fixation point, randomly between 1° and 360°, on each trial. In addition the stimuli could be flipped (i.e. we presented the mirror image). The luminance of the two curves was varied across trials and equaled 35, 60 or 95 cd/m^2 (Michelson contrasts were 32%, 54% or 75%), giving rise to total of 9 contrast combinations (Fig. 3B).

2.1.3. Procedure

Participants first engaged in a practice session to familiarize them with the task. They were instructed that they would first see a fixation cross, followed by the two curves and the colored markers. Their task was to indicate if the green or red marker fell on the target curve by pushing either the left or right button on the keypad (left and right buttons for red and green responses were counterbalanced across participants). Participants were asked to maintain fixation on a central point during the task and to respond as quickly and as accurately as possible. Once they indicated that they had received enough practice trials and understood the task, the first block began. They were instructed to rest between blocks and continue to the next block at their own pace, by pushing the space bar.

The time-course of an example trial is shown in Fig. 3C. The trial started with the presentation of a fixation cross for 300 ms and this was followed by the stimulus that remained on the screen until a response was given, or until 5000 ms had passed. We gave feedback at the end of each trial by presenting a symbol (size 0.5°) for 500 ms. A correct trial was followed by a green tick mark; an incorrect trial by a white cross and we presented a cartoon frowning face if the subject did not respond. Following each block participants saw a screen telling them to take a break – this also showed them their mean RT and correct rate (percentage) on the previous block of trials. The two curves were presented at one of three contrasts and there were three positions for the marker, resulting in a $3 \times 3 \times 3$ design. Each block (108 trials) consisted of four repetitions of each of the 27 conditions, and the order of these conditions was random within the block. Trials with incorrect responses were repeated later in the block. Each participant completed ten blocks,

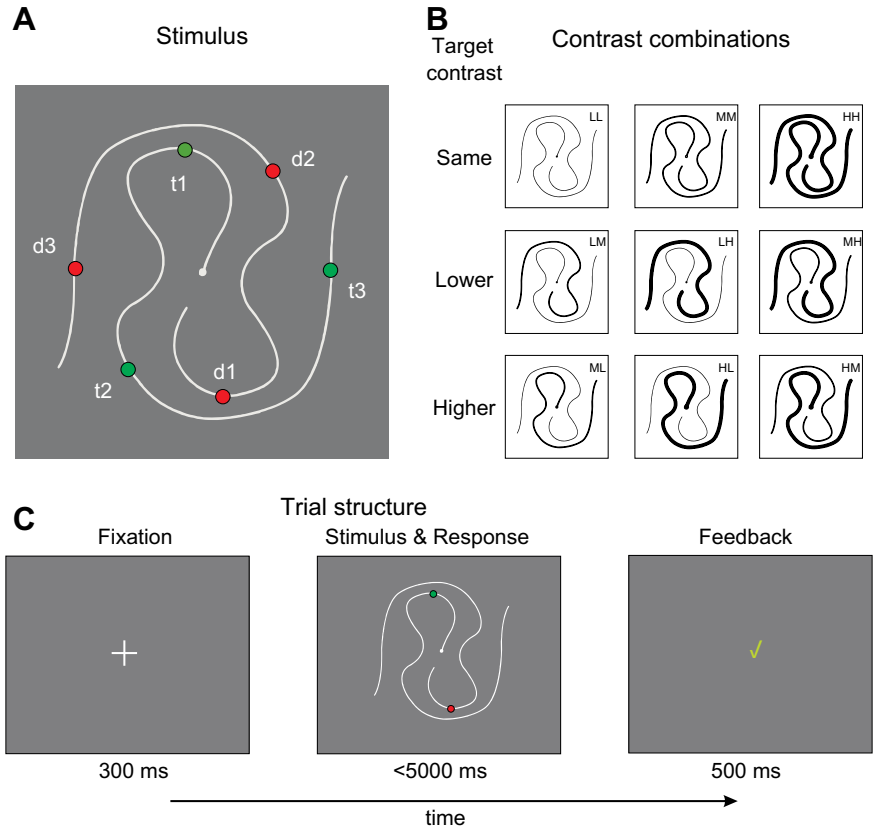

Fig. 3. Stimulus and design of Experiment 1. (A) The participant saw two curves. The target curve was connected to the fixation point, whereas the distractor curve was not. One marker was presented on the target curve and another marker on the distractor. Both markers appeared at the equivalent positions, i.e. on both curves either at position 1 (t1 and d1), position 2 (t2 and d2) or position 3 (t3 and d3). (B) The two curves were presented at either low (L), medium (M) or high (H) contrasts, resulting in nine contrast combinations. (C) Time course of one trial. The fixation cross was followed by the stimuli consisting of two curves and two markers (shown here at position 1). Feedback about accuracy was given after the response.

i.e. a total of 1080 correct trials with 40 correct trials per condition. We asked participants to maintain fixation on the fixation point but did not monitor eye movements. Previous studies demonstrated that the pattern of response times in the curve-tracing task is not strongly influenced by eye movements (McCormick & Jolicoeur, 1992; Roelfsema, Houtkamp, & Korjoukov, 2010).

2.1.4. Analysis

We used a repeated measures analysis of variance (ANOVA) for our statistical analysis and applied Greenhouse–Geisser corrections if appropriate (we report the original degrees of freedom). Incorrect trials were excluded as were trials with RTs over 3000 ms (0.7% of all correct trials).

2.2. Results

In accordance with previous curve-tracing studies (Jolicoeur, Ullman, & Mackay, 1986), the reaction time of the subjects increased approximately linearly with the length of the curve that had to be traced, with delays of several hundreds of ms. To highlight this serial tracing effect, our first analysis collapsed reaction time (RT) across contrast combinations (Fig. 4A). Average RT was 835 ms at the shortest distance, it increased to 953 ms at the intermediate distance and to 1160 ms at the longest distance. We next investigated the interaction between marker distance and contrast with a two-way ANOVA, with the three positions of the marker and nine possible contrast combinations of the two curves as factors (Fig. 4D). In accordance with Fig. 4A we obtained a significant main effect of marker position ($F(2,18) = 77$, $p < 10^{-5}$). In addition, we obtained a significant main effect of contrast combination ($F(8,72) = 24.5$, $p < 10^{-5}$) and a significant interaction between marker position and contrast combination ($F(16,144) = 7.16$, $p < 10^{-5}$). This interaction was driven by an influence of the contrast combination on tracing speed, which was higher if the contrast of the target curve was higher than that of the distracter (Fig. 4D).

To further investigate this interaction, we estimated the speed of curve-tracing (in ms per deg) by fitting lines to the RT-data for each of the nine contrast combinations (Fig. 4B and D). These lines accounted well for the pattern of RTs and explained an average of 98.4% of the variance of the across-subject average RTs (these lines explained on average 11% of the variance of individual RTs per subject – this lower value is caused by the intrinsic variance of RT distributions).

Are the differences in slope between conditions significant? To address this question, we carried out an additional one-way ANOVA on slopes, with contrast combination as the factor of interest. As expected, tracing-speed depended on contrast ($F(8,72) = 9.11$, $p < 10^{-4}$). A post hoc Tukey test showed that there were no significant within-group differences in tracing-speed when we grouped the data on the basis of whether the target curve had a higher (T > D), a lower (T < D), or the same contrast as the distractor (T = D) (Fig. 4B and C). In our next analysis we therefore collapsed the data within these three contrast combination groups and repeated the one-way ANOVA ($F(2,18) = 12.6$, $p < 10^{-4}$). As can be seen in Fig. 4B and C, tracing speed was fastest (i.e. the slope was smallest) if the target curve had a higher contrast than the distractor (T > D, Tukey post hoc test, $p < 10^{-3}$; group difference indicated

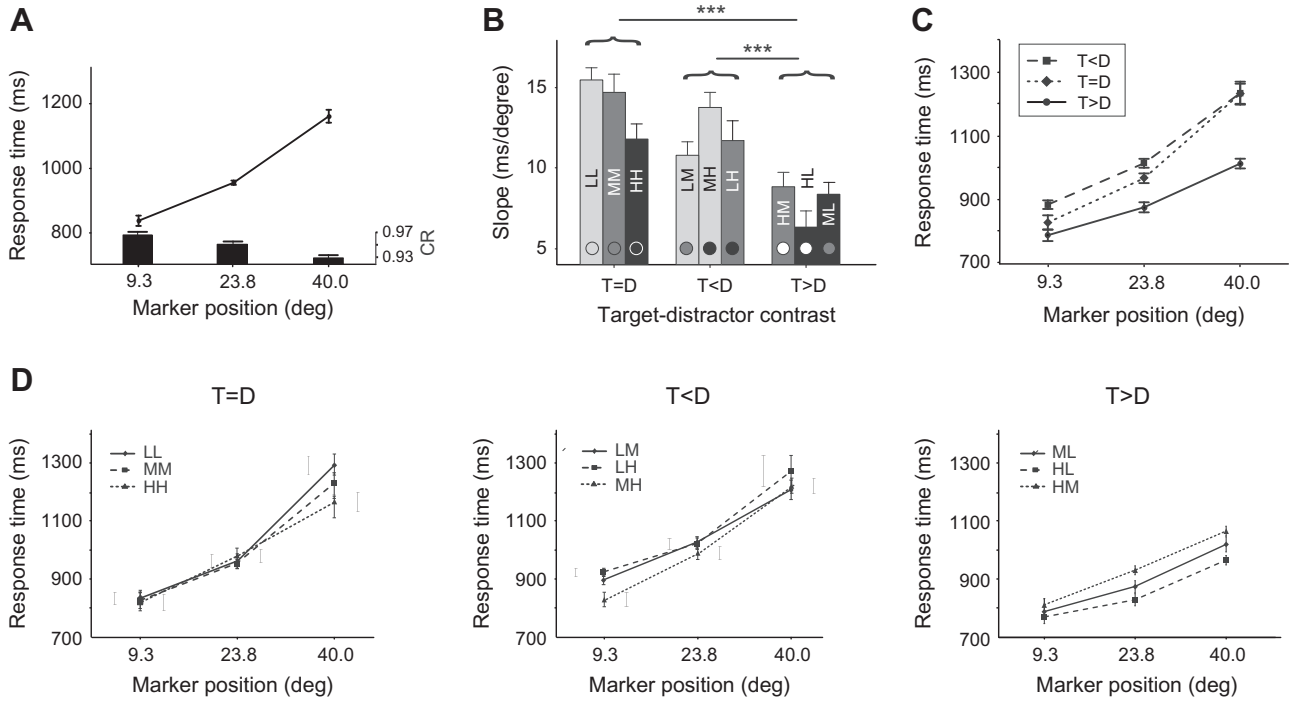

Fig. 4. Results of Experiment 1. (A) Average reaction times and accuracies (bars) for each of the three marker positions, collapsed across all contrast combinations. CR, correct rate. (B) Tracing speed in ms/deg for each contrast combination. Bar color represents the contrast of target curve, contrast of the distracter is indicated by the small circle. For the statistical analysis, the data was collapsed within the three contrast groups and tracing in the T > D group was significantly faster than the other groups (***; $p < 10^{-3}$). (C) Mean reaction times for each marker position, collapsed across contrast groups. Error bars represent standard error of the mean. (D) Reaction times as function of marker position for every contrast combination.

in Fig. 4B with ***), but the tracing speed when the curves had the same contrast (T = D) did not differ from the speed if the target curve had a lower contrast than the distracter (T < D, Tukey post hoc test, $p = 0.3$).

We investigated the subjects' accuracy with a 2-way ANOVA with position of the marker and contrast combination as factors. Accuracy decreased if the distance between the fixation point and the marker was larger ($F(2,18) = 11.04$, $p < 10^{-3}$). There was also a significant main effect of contrast combination on accuracy ($F(8,72) = 4.6$, $p < 5 \times 10^{-4}$) and a significant interaction ($F(16,144) = 2.6$, $p < 5 \times 10^{-3}$). We used a Tukey test to reveal the nature of this interaction. There were no significant differences in accuracy between contrast combinations at positions 1 and 2 ($> 5 \times 10^{-2}$) but there was a difference at marker position 3 because the subjects made most errors (9.4%) when the target curve had a lower contrast than the distracter (D < T), significantly more than in the T > D condition (4.5%; $p < 5 \times 10^{-3}$), whereas the difference with T = D condition was not significant (6.9%; $p = 0.12$). Error rates were higher when RT was longer, indicating that there was no speed-accuracy trade-off.

2.3. Discussion

We found that tracing speed was constant (about 15 ms/deg for the present set of stimuli) if the two curves have the same contrast, and that this speed did not depend strongly on the absolute luminance contrast. In addition, we found that the tracing speed was also similar if the target curve has a lower contrast than the distracter. However, the tracing speed increased if the target curve had a higher contrast than the distracter.

The results demonstrate that, compared to when both curves were of the same contrast, tracing was not impeded when a low contrast target curve had to be traced in the presence of a high contrast distracter (see also McCormick & Jolicoeur, 1992). The results suggest that tracing speed is even slightly faster in the presence of a distracter with higher contrast, although this effect did not reach statistical significance (Fig. 4B). One candidate mechanism for the separate coding of attention and contrast is that the strength of the attentional effect depends on the difference in activity between an attended and non-attended curve (yellow region in Fig. 2D–F). Within the contrast range tested in Experiment 1, we did not observe differences in tracing speed if both curves had a low, intermediate or high contrast.

These results also suggest that the efficiency of curve-tracing increases if the target curve is of uniquely high contrast. One possible explanation is that participants might have used a strategy other than curve tracing if the two curves are of different luminance (McCormick & Jolicoeur, 1992). They could first determine the contrast of the target curve near fixation and then search for the marker on a contour element with the same contrast. This strategy would presumably give rise to a slope of zero, because the marker positions were all equidistant from the fixation point. Our results suggest that such a 'look-up' strategy, if it was used, may have been more efficient or more frequently used when the contrast of the target curve was highest.

The look-up strategy is only possible if the target curve has a unique contrast that differs from all distractors. Our second experiment addressed the contribution of this strategy and we therefore included a third curve, creating conditions where the target curve had the same contrast as zero, one or two distractors. Furthermore, the lowest contrast used in Experiment 1 was 32% (Michelson contrast), which is high if compared to previous psychophysical studies on the interaction between attention and contrast and also if compared to the aforementioned neurophysiological studies (Fig. 2D–F). In the second experiment we therefore increased the differences in contrast between the curves and used contrasts where models of the interaction between attention and contrast yield different predictions.

3. Experiment 2: The influence of contrast when tracing one of three curves

To discourage participants from using strategies other than contour grouping, we modified the paradigm to ensure that in most of the trials at least one other curve had the same contrast as the target curve, forcing them to rely on the serial tracing process. We also increased the difference between contrasts and used contrast values in the neurophysiologically interesting range. Will subjects be able to efficiently trace a target curve of very low contrast if it is accompanied by a distractor of much higher contrast?

3.1. Methods

3.1.1. Participants

Ten participants were recruited (7 females, average age: 22.3 years). They had normal or corrected to normal vision and had not participated in curve tracing tasks before. We obtained informed consent in writing before the experiment began.

3.1.2. Stimuli and apparatus

The apparatus was the same as in Experiment 1. The stimuli now consisted of three curves (4 pixels thick, anti-aliased) one of which was connected to a fixation point (the target curve) and three differently colored markers (Fig. 5A). The curves were presented on a gray background with a luminance of 15 cd/m^2. The curves had at a luminance of either 18.3 cd/m^2 or 85 cd/m^2 resulting in Michelson contrasts of 10% and 70%, respectively.

We presented either a red, blue or green marker on each curve at the equivalent positions, i.e. all three close to the fixation point, halfway the end of the curve or close to the end. The distance measured along the target curve from the fixation point to the marker at position 1 was 15.3°; the distance between positions 1 and 2 was 9.8° and the distance between positions 2 and 3 was 12.4°. All marker positions were equidistant from the fixation point on the circumference of an invisible circle with a radius of 7.5°.

The three curves were presented at one of two contrasts (Fig. 5B shows all contrast combinations) and there were three positions of the marker. Thus, there were either zero, one or two distractor curves with the same contrast of the target, resulting in a $2 \times 3 \times 3$ (contrast of target curve $\times$ number of distractors with same contrast $\times$ marker position) design. The structure of the trial was the same as in Experiment 1 (Fig. 5C). Each block (120 trials) consisted of five repetitions of each condition (8 contrast combinations $\times$ 3 marker positions), and the order of conditions within a block was random. Conditions with an incorrect response were repeated before the end of the block. Each participant completed eight blocks with a total of 960 correct trials and 40 correct trials in each of the conditions.

3.1.3. Procedure

All instructions and procedures were the same as in Experiment 1 except that we now told participants that they would see three curves (with the target curve connected to the central fixation point) and three colored markers. They had to decide if the marker on the target curve was green, red or blue and push the corresponding button on a keypad (the assignment of buttons for red, green and blue were counterbalanced across participants).

3.1.4. Analysis

We used the same statistical procedures as in Experiment 1. Incorrect trials and trials with reaction times over 3000 ms were excluded (only 0.02% of all correct trials). We collapsed the data across similar contrast combinations (e.g. HHL and HLH in Fig. 5B) resulting in three contrast combinations for the high contrast target curve and three for the low contrast target curve; zero, one or two distracter curves had the same contrast as the target curve.

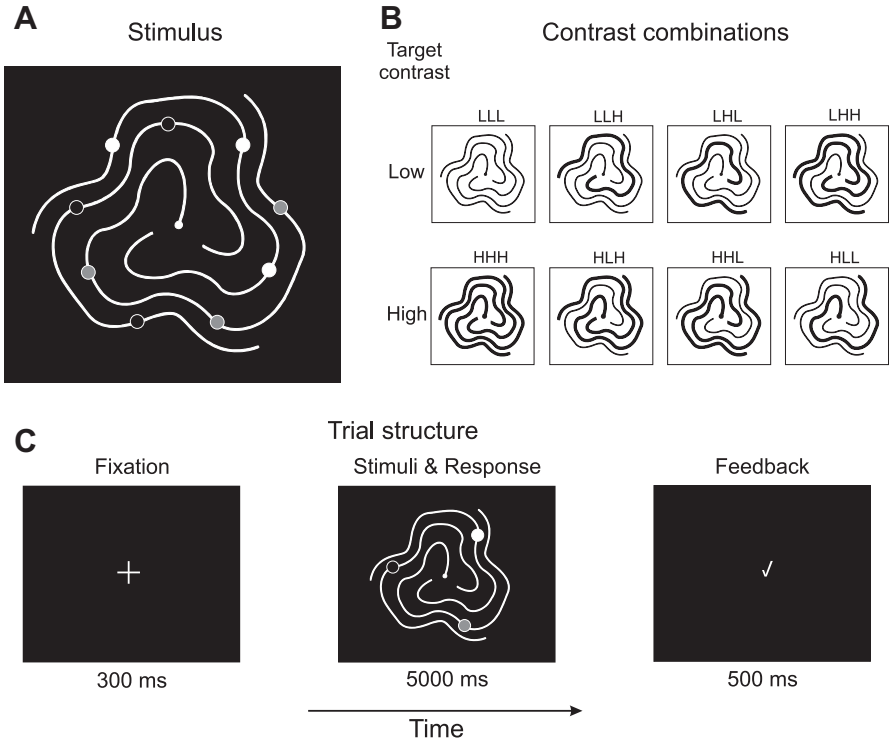

Fig. 5. Design and stimuli of Experiment 2. (A) The participant saw three curves with only the target curve connected to the fixation point. Markers were presented on each curve at either position 1, 2 or 3; all possible marker positions are indicated. (B) Each curve was presented at a low (L) or high (H) contrast, resulting in eight contrast combinations. (C) Time course of one trial. The fixation cross was followed by the stimulus with three curves and three markers (shown here at position 2).

3.2. Results

As expected, the RT increased for markers that were farther along the curve, in accordance with a serial tracing process (Fig. 6A, data collapsed across all contrast combinations). The mean RT at marker position 1 was 1209 ms, it increased to 1387 ms at position 2 and to 1733 ms at position 3. A two-way ANOVA with the three marker positions and the six contrast combinations of the two curves as factors confirmed a main effect of marker position ($F(2,18) = 283.9$, $p < 10^{-5}$) and we also observed a main effect of contrast combination ($F(5,45) = 45.8$, $p < 10^{-5}$). The participants were faster with fewer distractor curves with the same contrast as the target curve, resulting in a significant interaction between marker position and contrast combination ($F(10,90) = 28.0$, $p < 10^{-5}$) (Fig. 6C).

To investigate the interaction between marker position and contrast, we estimated the speed of curve tracing (in ms/deg) by fitting a line to the within-subject RT data for each of the six contrast combinations. The linear fit to the pattern of RTs as function of marker position was excellent because it accounted for an average of 97.6% of the variance of the pattern of average RTs across subjects (and on average 19% of the variance of the single-trial RT distributions – a lower value because of the high variance of the RT distributions). We analyzed how tracing speed depended on contrast with an additional two-way ANOVA with two levels of the target curve (low/high contrast) and three levels pertaining to the number of distracter curves with the same contrast as the target curve (0, 1 or 2). This analysis revealed a significant main effect of target curve contrast ($F(1,9) = 52$, $p < 10^{-4}$) because participants tended to trace faster if it was high (Fig. 6B and C). There was also a main effect of the number of distracter curves of the same contrast as the target curve ($F(2,18) = 65$, $p < 10^{-5}$). Participants were slowest at tracing (40 ms/deg) when the two distracters curves were of the same contrast as the target curve, they were significantly faster when one of the distracters differed from the target (31 ms/deg, $p < 10^{-3}$; *** in Fig. 6B) and fastest when the target curve contrast was unique (18 ms/deg, $p < 10^{-3}$). We also obtained a significant interaction between target curve contrast and the number of distractors with the same contrast ($F(2,18) = 11$, $p < 5 \times 10^{-3}$), because the shortening of RT with the number of different distractors was most pronounced for the high contrast target curve. There was no difference in the slope between high and low contrast target curves if the two distracters had the same contrast as the target (post hoc Tukey test, $p > 0.5$, Fig. 6B and C, left panel).

To investigate accuracy, we used 3-way ANOVA with position of the marker, contrast of the target curve (high/low) and number of distracters of the same contrast (0, 1 or 2) as factors. Accuracy decreased when the distance between the fixation point and the marker was larger ($F(2,18) = 12.6$, $p < 5 \times 10^{-4}$). There was no main effect of the target curve contrast but there was a main effect of the number of distracters with the same contrast as the target, as accuracy was higher when contrast of the target curve was unique ($F(2,18) = 5.9$, $p < 0.05$). There were significant interactions between the number of distracters of the same contrast as the target curve and target curve contrast ($F(2,18) = 5.2$, $p < 0.05$) as well as position ($F(4,36) = 6.7$, $p < 5 \times 10^{-4}$). Performance was worst if the target curve was of low contrast and one of the distracters was of high contrast (6.6% errors), whereas accuracy was highest if target curve contrast was unique (2% errors). These results are inconsistent with a speed-accuracy trade-off.

3.3. Discussion

These results replicate and extend the findings of Experiment 1 with larger contrast differences and with three curves. Tracing speed was not affected by the contrast of the target curve if all curves had the same contrast. Apparently, the efficiency of the mechanisms responsible for the spread of object-based attention along the target curve does not depend strongly on luminance con-

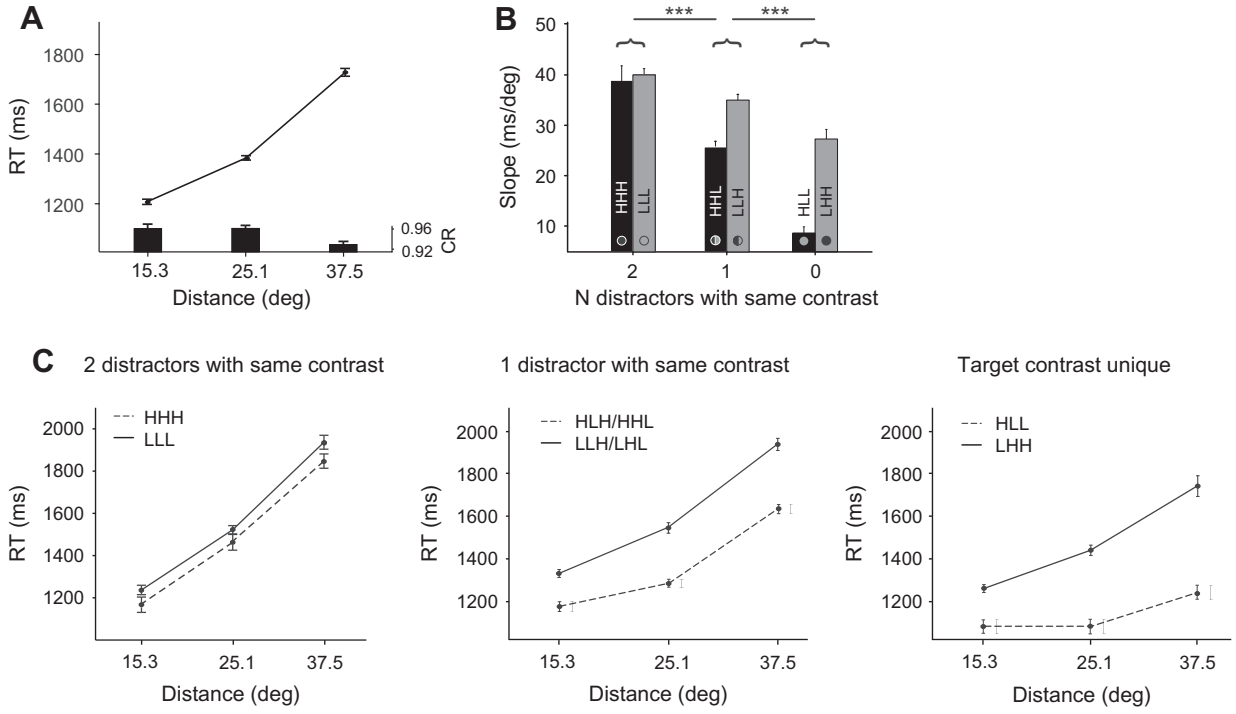

Fig. 6. Results of Experiment 2. (A) Average reaction times and accuracies (bars) for each of the three marker positions, collapsed across all contrast combinations. CR, correct rate. (B) Mean tracing time in ms per visual degree, for each contrast combination. The gray value of the bars represents the contrast of the target curve and the contrast of the two distracter curves is shown by the small circle. For the statistical analysis data was collapsed within three contrast groups and tracing speed was significantly different between groups (***, $ps < 10^{-3}$). (C) Average reaction time as function of marker positions for every contrast combination. Error bars represent standard error of the mean.

trast. The slope of the RTs in Experiment 2 was approximately 40 ms/deg if all curves had the same contrast, whereas it was approximately 15 ms/deg in Experiment 1. This slower tracing speed is in accordance with Jolicoeur, Ullman, and Mackay (1991) who demonstrated that tracing speed is proportional to the distance between curves. The distance between the three curves of our Experiment 2 was smaller than the distance between the two curves of Experiment 1 and the time required to trace one degree of visual angle therefore increased.

In addition, the results confirm that in comparison to the situation where all curves have the same contrast, distracter curves with a higher contrast than the target curve do not impair tracing. The spread of object-based attention is not dominated by stimuli with a high contrast. Instead, we observed that high contrast distractors interfered less with tracing of a low contrast target curve than did low contrast distractors. A similar effect occurred if the target curve had a high contrast, where tracing speed increased if the distractors were of low contrast. In this situation, the benefit of distractor curves with a different contrast was even larger, even if one of the distractor curves had the same contrast as the target, a stimulus that precludes the look-up strategy because in this situation luminance contrast does not uniquely differentiate the target curve from the distractors. How can we explain the higher tracing speed in this condition?

One possible explanation is inspired by the finding that tracing speed increases if the distance between curves is larger (Jolicoeur, Ullman, & Mackay, 1991). The mechanism that determines the effective distance between curves might be sensitive to the contrast of the curves. Thus, a low contrast distractor might not be seen by this mechanism if the target curve has a high contrast so that the effective distance between the target curve and the other curves is larger and tracing speed increases. The finding that tracing speed for low-contrast target curves increased less if the distractors were of high contrast might be explained by an asymmetry in this mechanism that might take distractor curves with a higher contrast than the target curve into account. The effective distance between curves would therefore be smaller if the contrast of the target curve is lower than that of the distractors. The general discussion will further elaborate on the putative mechanisms that are sensitive to the effective distance between curves.

4. Experiment 3: Tracing curves with different contrast polarities

Experiments 1 and 2 revealed that tracing speed increases if the distractor curves have a contrast that differs from the target curve. Our last experiment will investigate the effect of contrast polarity. If the absolute contrast level determines tracing speed then it might be predicted that the contrast polarity has little effect on tracing speed. On the other hand, it is also conceivable that the tracing process can discard distractors with an opposite contrast polarity as easily as distractors with a lower contrast. This result would be in accordance with previous studies showing that tracing also speeds up if the target curve differs from the distractors in color (Houtkamp & Roelfsema, 2010; Jolicoeur, Ullman, & Mackay, 1991). To investigate the effect of contrast polarity on curve tracing speed, we repeated the 3-curve experiment with black and white curves presented on a gray background.

4.1. Method

4.1.1. Participants

Ten participants were recruited (8 women and 2 men with a mean age of 22.4 years). All had normal or corrected-to-normal vision and had not participated in curve tracing tasks before. Written informed consent was obtained before the experiment began.

4.1.2. Stimuli, apparatus and procedure

The stimuli, apparatus and procedure were as in Experiment 2, except that the three curves were presented on a brighter gray background (50 cd/m^2). The curves could be either darker (30 cd/m^2) or lighter (85 cd/m^2) with a positive or negative 26% Michelson contrast (Fig. 7A). Trials with an incorrect response were repeated before the end of the block. Each participant completed eight blocks with 120 trials per block, resulting in a total of 960 correct trials and 40 correct trials per condition. Statistical analysis procedures were the same as in previous experiments.

4.2. Results

The task invoked a serial tracing process because RT increased for the marker positions farther along the target curve, just as in the previous experiments (Fig. 7B). A two-way ANOVA with the three positions of the marker and the six contrast polarity combinations of the two curves as factors revealed significant main effects of marker position ($F(2,18) = 167$, $p < 10^{-5}$), contrast polarity combination ($F(5,45) = 31.0$, $p < 10^{-5}$) and a significant interaction between these factors ($F(10,90) = 13.0$, $p < 10^{-5}$).

To investigate this interaction, we fitted lines to the within subject RTs as function of marker position to estimate the tracing speed (ms/deg) for each of six polarity combinations. The fit accounted for an average of 97.9% the variance when we averaged the data across participants in each of the conditions (at the single trial level the fits accounted for an average of 16% of the variance, due to the high variance of RT distributions). The tracing speed was analyzed with an additional two-way ANOVA with two levels of target curve contrast polarity (positive/negative) and three levels pertaining to the number of distracter curves with the same contrast polarity as the target curve (0, 1 or 2). This analysis did not reveal a significant main effect of target curve contrast polarity ($F(1,9) = 4.3$, $p > 0.05$), but the effect of the number of distracters with the same contrast polarity was significant ($F(2,18) = 35.6$, $p < 10^{-5}$) (Fig. 7C). The tracing speed increased with fewer distracter curves with the same contrast polarity as the target curve. It was 33 ms/deg when both distracters had the same contrast polarity as the target curve, it was significantly faster (26 ms/deg, $p < 0.005$, Post hoc Tukey test) with one distracter of the same contrast polarity and even faster (19 ms/deg, $p < 0.005$) when none of the distractors had the same contrast polarity (*** in Fig. 7C).

To investigate accuracy, we used 3-way ANOVA with marker position, target curve polarity and the number of distracters of the same polarity as the target curve as factors. Accuracy decreased if the distance between the fixation point and the marker was larger ($F(2,18) = 7.2$, $p < 0.01$). There was no main effect of target curve contrast polarity, but a main effect of the number of distracters with the same contrast polarity ($F(2,18) = 12.66$, $p < 5 \times 10^{-4}$). Accuracy was highest when the contrast polarity of the target curve was unique (2% errors). Finally there was an interaction between marker position and number of distracters with the same contrast polarity ($F(4,36) = 2.8$, $p < 0.05$). Accuracy at position 3 was lowest when one of the distracter curves had a contrast polarity that matched that of the target curve (4.6% errors).

4.3. Discussion

These results demonstrate that reversing contrast polarity of all curves has little effect on the spread of visual attention along the curve. Tracing becomes more efficient when distracters have the opposite contrast polarity as the target curve, resembling the effect of a difference in contrast between curves observed in Experiment 2. Unlike Experiment 2, however, we did not see an asymmetrical advantage for either positive or negative contrast polarity. The tracing of a target curve with a contrast polarity that differs from

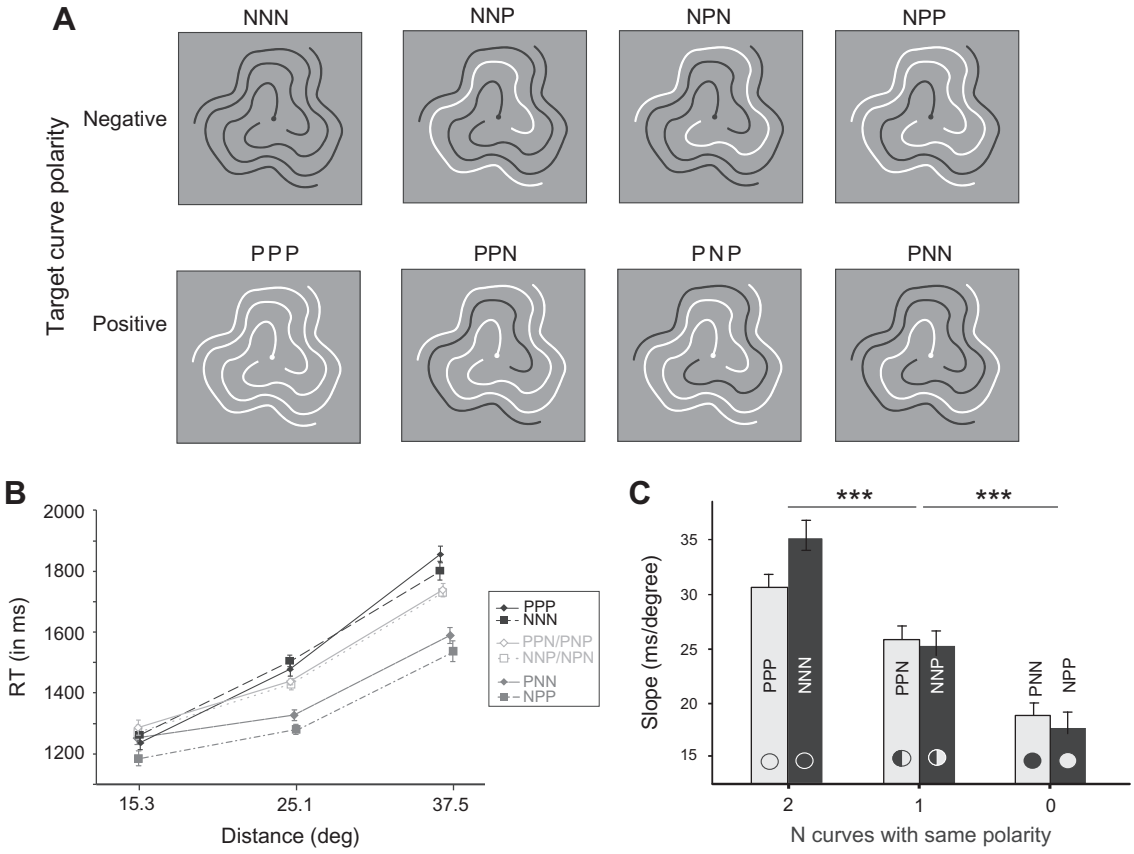

Fig. 7. Stimulus design and results of Experiment 3 that tested the effect of contrast polarity. (A) Stimulus configuration and eight possible contrast polarity combinations. (B) Average reaction times for each of the three marker positions, for every contrast polarity combination. (C) Mean tracing time (in ms/deg) for each contrast polarity combination. The statistical analysis revealed a main effect of number of distracters with opposite polarity (***, $p < 0.005$). Bar shading represents the target curve contrast polarity and the polarity of the two distracter curves is indicated in the small circle. Error bars represent standard error of the mean.

that of the distracters appears to be as efficient as the tracing of a target curve with a different color (Houtkamp & Roelfsema, 2010; Jolicoeur, Ullman, & Mackay, 1991).

The previous studies that tested the influence of a difference in color between the target and distractor curve on tracing speed used two curves. Such a task can be solved with a look-up strategy, e.g. registering the color of the target curve where it is cued (usually at the fixation point) and then looking for the marker on the curve with the same color. However, this look-up strategy was not possible in our conditions with only a single distractor curve with the same contrast polarity as the target curve. Yet, tracing speed also increased significantly in this condition. This increased tracing speed might be caused by an increase in the effective distance between the target curve and the remaining distractors with the same contrast polarity. The curves with opposite contrast polarity may carry less weight for the mechanism that determines the effective distance between the target curve and the adjacent distractors so that the tracing speed increases.

5. General discussion

The present study investigated the effect of variations in contrast and contrast polarity on the efficiency of attentional selection in a contour-grouping task. Previous work demonstrated that subjects solve this task by gradually spreading object-based attention along the representation of the target-curve (Houtkamp, Spekreijse, & Roelfsema, 2003; Scholte, Spekreijse, & Roelfsema, 2001). We found that when target and distracter curve(s) were of matched contrast, the speed of the spread of attention was unaffected by the absolute contrast of the curves (as in Experiment 4 in McCormick & Jolicoeur, 1992) and variations in contrast polarity did not affect the speed of tracing either. Furthermore, compared to this 'matched' condition, the spread of object-based attention along a low or intermediate curve was not impeded by the presence of high contrast distracters. Instead, we observed an increase in the efficiency of the contour grouping process if distractors had a higher contrast than the target curve. These results offer new insights into the relationship between object-based attention and luminance contrast.

5.1. Interactions between attention and luminance contrast

The nature of the interaction between luminance contrast and spatial attention has been intensely debated in the neurophysiological and psychophysical literature in recent years. A number of psychophysical studies demonstrated convincingly that attention causes a small increase in the perceived contrast of a stimulus (Carrasco, Ling, & Read, 2004; Ling & Carrasco, 2006; Störmer, McDonald, & Hillyard, 2009). Other studies observed only weak effects of attention on perceived contrast (Palmer & Moore, 2009; Prinzmetal et al., 1997; Schneider, 2006; Schneider & Komlos, 2008), but some of these discrepancies presumably reflect differences in experimental design (Anton-Erxleben, Abrams, & Carrasco, 2010; Carrasco, Fuller, & Ling, 2008; Ling & Carrasco, 2007; Liu, Abrams, & Carrasco, 2009).

Our data support the predictions of the additive model (Fig. 2) and aligns with neurophysiological data implying that the neuronal codes for attention and contrast are largely distinct. The con-

trast values in our experiments were far apart so that none of the aforementioned studies would have predicted that attention increased the perceived contrast of the low contrast curves to a level higher than that of a non-attended high-contrast curve. Nevertheless, subjects did not experience difficulties in tracing the low contrast curves, even if they were accompanied by curves with a higher contrast. Thus, an increase in perceived contrast is unlikely to be the mechanism by which visual attention operates in the object-based attention task used in this study, although our results are not incompatible with attention causing moderate changes in the subjective perception of contrast. Thus, observers can select stimuli with a low contrast that still have a lower contrast in perception than other curves once they are attended (the reader can verify this in Fig. 2A by tracing the low contrast curve). This result is in accordance with visual search tasks where subjects do not experience difficulties in the selection of low contrast target items flanked by items with a higher contrast and can even specifically search for low contrast items (Einhäuser, Rutishauser, & Koch, 2008; Einhäuser & König, 2003; Navalpakkam & Itti, 2006; Pashler, Dobkins, & Huang, 2004). These separable influences of contrast and attention on our perception must have a neuronal correlate. How does the visual system separate the codes for luminance contrast and attention, two factors that both increase neuronal activity?

There is parallel debate on the interaction between spatial attention and luminance contrast in neurophysiology. In the introduction we mentioned the contrast-gain model, which holds that attention causes a shift of the neuronal contrast response function to the left (Fig. 2D) (Reynolds, Pasternak, & Desimone, 2000; Treue, 2004). A strict interpretation of this model (a straw man) might predict that the effect of attention on neuronal activity is equivalent to an increase in perceived contrast. This strict interpretation of the contrast-gain model would hold that an unattended curve with a high contrast evokes the same activity in visual cortex as an attended curve of lower contrast. If the only effect of object-based attention in visual cortex were to shift the contrast response function, then it might be difficult to group image elements with intermediate contrast in the presence of high contrast stimuli. Our results are not in accordance with this view. The efficiency of tracing low or intermediate contrast curves did not decrease in the presence of high contrast distracters. The ability to attend stimuli irrespective of contrast implies that the neuronal codes for attention and contrast are separable. Previous studies suggest that curve-tracing is implemented in the visual cortex by the propagation of enhanced neuronal activity along the representation of the target curve (Roelfsema, Lamme, & Spekreijse, 2004; Roelfsema, 2006), and these attention shifts can also be measured in human observers with EEG (Lefebvre, Jolicoeur, & Dell'Acqua, 2010; Lefebvre et al., 2011). The visual system apparently can propagate the attentional response modulation if stimuli in a display differ in contrast.

Pooresmaeili et al. (2010) showed that it is possible to represent the contrast of a stimulus as well as the focus of attention with a population of neurons in the primary visual cortex (V1) of monkeys engaged in the curve tracing task illustrated in Fig. 8A. Some neurons (A-cells, where A denotes sensitive to attention) increased their activity for higher contrasts and also if attention was directed to the curve in their receptive field (Fig. 8B and C). Other neurons (N-cells) were only sensitive to contrast but did not change their response during attention shifts (Fig. 8D). The representation of contrast relied on N-cells whose activity was little influenced by attention. The representation of attention involved a comparison between the activity of A and N-cells. If attention was directed to the curve in the RF, A-cells increased their activity relative to N-cells and this response difference signaled attention.

If the difference between the activities of A and N-cells indeed determines attentional selection, then this difference signal could be propagated along the relevant curve (Fig. 2C) (Roelfsema & Houtkamp, 2011). If this model is correct, the efficiency of the propagation of object-based attention along the target curve should depend on the strength of this difference signal (the yellow area in Fig. 8B). The three models of the interaction between contrast and attention therefore make different predictions about how contrast variations influence the efficiency of this process. According to the contrast-gain model, attentional modulation is strongest at low contrasts (Fig. 2D) (Martınez-Trujillo & Treue, 2002; Reynolds, Pasternak, & Desimone, 2000), the response-gain model holds that modulation is strongest at higher contrasts (Fig. 2E) (Williford & Maunsell, 2006) and the additive model that the attentional effect is relatively constant across contrast levels (Fig. 2F) (Buracas & Boynton, 2007). Studies in area V1 of monkeys performing the curve-tracing task demonstrated that the amplitude of the response modulation does not depend strongly on contrast (Fig. 8B) (Pooresmaeili et al., 2010; Thiele et al., 2009), which is in accordance with an additive model. The present psychophysical results are also in support of the additive model, because we found that the efficiency of the contour grouping process is relatively invariant to variations in luminance contrast, at least under conditions where the target curve is of the same or lower contrast as the distracters.

In the curve-tracing task, object-based attention spreads according to the Gestalt criteria of good continuation and connectedness. Neurons in visual cortex and interconnected subcortical structures (Purushothaman et al., 2012) are tuned to orientation and to precise position of contour elements, response properties that are useful for the propagation of enhanced activity along a curve. Indeed, attentional response modulation in visual cortex does spread according to the Gestalt grouping rules (Wannig, Stanisor, & Roelfsema, 2011). Our focus on visual cortex does not exclude a contribution of the so-called "fronto-parietal attention network" that plays a role in many tasks that require attention shifts (Corbetta & Shulman, 2002). However, it is not clear if neurons in this fronto-parietal network are tuned in a manner that could ensure that the attentional selection signals stay on the target curve and do not spread to distractors, especially if they are nearby. Future studies may determine the relative contribution of the visual cortex and areas of the frontal and parietal cortex as well as the interactions between visual, parietal and frontal brain regions for the control of object-based attention (see also Khayat, Pooresmaeili, & Roelfsema, 2009).

5.2. Variations in the speed of contour integration

In some of the conditions tracing was not necessary because subjects could have used a look-up strategy. Participants could have registered the contrast of the curve nearest to the fixation point and then have searched for the marker on the curve with the same contrast. Experiments 2 and 3 therefore introduced a third curve discouraging this strategy in most of the trials. We observed that tracing speed increased if one of the distractor curves had the same contrast as the target and the other curve differed in contrast. A possible explanation for this benefit is that the difference in contrast increases the effective distance between the target curve and the nearest distractor. To explain this effect and the notion of 'effective distance' we will briefly consider the relation between tracing speed and the distance between curves.

Jolicoeur, Ullman, and Mackay (1991) demonstrated that tracing speed increases if the distance between the target curve and the distractors is larger. As a result, curve tracing is largely scale-invariant. Consider, for example, the stimulus of Fig. 3C. If the stimulus is viewed from a distance of 40 cm, it takes approximately 800 ms to trace from the fixation point to the green marker (Fig. 4A). If the same stimulus is viewed from a distance of

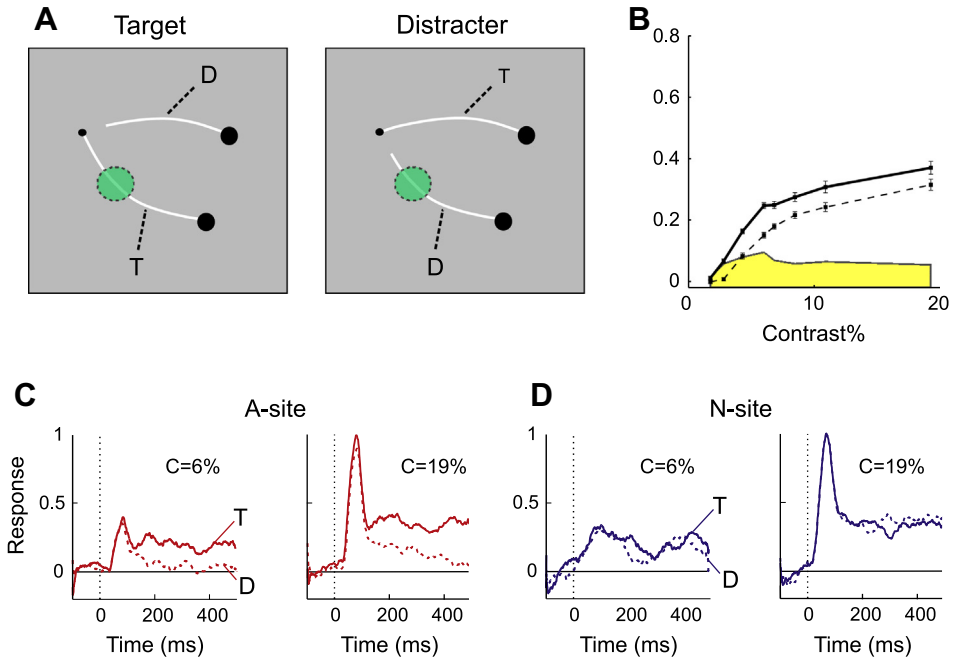

Fig. 8. Neuronal activity in area V1 of the visual cortex of monkeys during curve tracing. (A) The monkeys traced a curve connected to the fixation point and planned an eye movement to the end of this target curve (T). The other curve was a distractor (D). Green circle shows the position of the receptive field of the V1 cells. (B) Neuronal activity evoked by the target curve (continuous line) and distractor curve (dashed line) as function of contrast. The yellow area denotes the attentional modulation, which is the difference in activity evoked by an attended and non-attended curve. (C) Example V1 multi-unit recording site where neurons increased their activity if the contour element was attended (A-site) for curves with a contrast of 6% and 19%. (D) Example N-site where neurons coded the contrast of the stimulus but were uninfluenced by attention shifts. Reproduced with permission from Pooresmaeili et al. (2010).

80 cm, subjects have to trace half the distance in degrees of visual angle but the distance between the target and distractor curve is also twice as small. Jolicoeur and Ingleton (1991) demonstrated that the RT is the same in these two conditions, because the tracing speed (in degree/s) is proportional to the distance between the curves (Jolicoeur, Ullman, & Mackay, 1991). Thus the influence of a decrease in the length of the curves viewed from a larger distance on response time is compensated by the reduced tracing speed due to the smaller distance between the curves.

To explain scale invariance, Roelfsema and Singer (1998) proposed that the propagation of the attentional response modulation takes place in multiple areas of the visual cortex (see also Edelman, 1987; Roelfsema & Houtkamp, 2011). If curves are far apart, the tracing process makes fastest progress in higher visual areas with larger receptive fields (Fig. 9A). Higher areas are thought to also feed the attentional response enhancement back to the lower visual areas where the propagation proceeds faster than would have been possible without the higher areas (small receptive fields in Fig. 9A). If curves are nearby, however, the large receptive fields in higher areas fall on multiple curves and the enhanced response might spill over to distractor curves (dashed receptive fields in Fig. 9A and B). This calls for a mechanism that blocks the propagation in the higher areas whenever multiple curves fall into one receptive field (Jolicoeur et al., 1991; Edelman, 1987; Roelfsema & Singer, 1998). The propagation has to be taken over by lower visual areas with smaller receptive fields, which fall on only a single curve. The higher spatial resolution causes a decreased grouping speed because in early visual areas more synapses have to be crossed to bridge the same distance in the visual field. Unpublished data from our lab shows that the delays in the propagation of the enhanced response in the visual cortex during curve-tracing indeed increase if the distance between curves is smaller (Pooresmaeili & Roelfsema, in preparation). The enhanced response in the monkey visual cortex propagates at a speed of approximately 50 ms per receptive field, which is in the same range as the value of 80–100 ms predicted on the basis of psychophysical data (Jolicoeur, Ullman, & Mackay, 1991).

In the present study we observed an intriguing asymmetry in the benefit caused by curves with a contrast that differed from that of the target curve (Fig. 6B). High contrast distractors interfered more with the tracing a low contrast curve than low contrast distractors did with the tracing of a high contrast curve. This result suggests that the mechanism sensitive to the distance between the curves, blocking the propagation in higher visual areas and thereby determining tracing speed, ignores curves with a lower contrast (Experiment 2) than the target curve or with the opposite contrast polarity (Experiment 3). However, this mechanism seems to be sensitive to distractors with a higher contrast than the target curve. As a result, tracing of a low-contrast target curve accompanied by high contrast distractors might occur in a lower visual area than the tracing of a high-contrast curve accompanied by low-contrast distractors (Fig. 9C). Albeit speculative, this asymmetry would explain the smaller increase in tracing speed if distractors have a higher contrast than the target curve. The precise mechanism that blocks the propagation of attentional response modulation in higher visual areas if curves are nearby is not well understood. This mechanism and its relation to the rich literature on visual masking and crowding could be explored in future work. Indeed, in crowding a similar asymmetry occurs, because crowding is strong if the target has a lower contrast than the interfering flankers, whereas crowding is weak if target contrast is higher (Kooi et al., 1994; Chung, Levi, & Legge, 2001).

5.3. Incremental contour grouping and its relation with object-based attention

Curve-tracing is a task that requires subjects to explicitly report whether two contour elements are part of a single elongated curve. In other words, it is a 'binding-task', requiring the perceptual grouping of image elements that belong to a single, spatially ex-

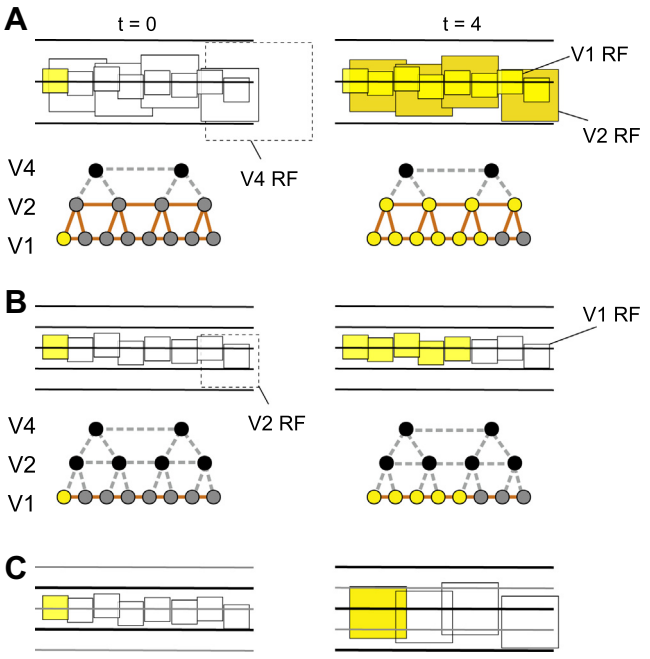

Fig. 9. Scale invariance of contour grouping. (A) Scale invariance of contour grouping can be explained if the propagation of enhanced neuronal activity takes place at different spatial scales, in multiple areas of visual cortex that represent curves at different spatial resolutions. In this example, the V2 receptive fields fall on only a single curve and the propagation of enhanced activity in V2 is therefore faster than in V1. Feedback connections from V2 to V1 ensure that the activity of V1 neurons is also enhanced (yellow circles). Black circles denote V4 neurons with multiple contour elements in their RFs which are even larger (dashed rectangle) and cannot participate in incremental grouping. (B) With a narrower spacing of the curves, V2 neurons cannot propagate the attentional response modulation so that V1 takes over and the speed of contour grouping decreases. Orange (gray dashed) lines denote connections within and between areas between neurons that can (cannot) propagate the enhanced response. (C) Left, during tracing of a low contrast curve, high contrast curves appear to block the propagation of attentional response modulation in higher areas. Right, low contrast curves may interfere less with the propagation of attentional response modulation in higher visual areas.

tended object (Roelfsema, 2006). The elementary features of a visual stimulus, like its many contours but also its color and motion are initially registered in separate cortical areas. We previously proposed that there are two complementary mechanisms for feature binding (Roelfsema, 2006; Roelfsema & Houtkamp, 2011). The first 'base-grouping' mechanism relies on the tuning of neurons in object selective cortex to specific feature combinations that define complex objects (Freiwald, Tsao, & Livingstone, 2009; Tsao, 2006) and is highly efficient (Thorpe, Fize, & Marlot, 1996). However, base-grouping appears not to resolve all binding problems. If the configuration unfamiliar as is the case for the contorted curves of the curve-tracing task, there may be no neurons that code the required feature conjunctions. In these situations, the features of the unfamiliar object can still be grouped in perception, by labeling them at lower levels of representation with object-based attention that gradually spreads over the target curve, a process that is called 'incremental grouping' (Roelfsema, 2006). In the curve-tracing task, the incremental grouping process relies on the Gestalt grouping cues of connectedness and good continuation (Wertheimer, 1923). The enhanced neuronal response ('attentional modulation') spreads among neurons in the visual cortex coding collinear and connected line elements (Roelfsema, 2006; Wannig, Stanisor, & Roelfsema, 2011), while at a psychological level of description, object-based attention spreads over the contour elements that belong to the target curve. Here we have shown that this incremental grouping process occurs with a constant efficiency for objects with different luminance contrasts, and that it is not dominated by objects with a contrast that is higher than the object that is of relevance for the task.

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